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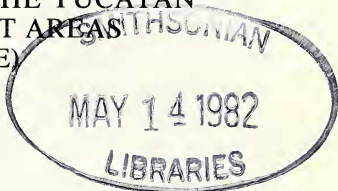
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ARTICLE 1

## PARALLEL GEOGRAPHIC VARIATION IN THREE *MYIARCHUS* FLYCATCHERS IN THE YUCATÁN PENINSULA AND ADJACENT AREAS (AVES: TYRANNIDAE)

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### ABSTRACT

Within the large range of the tyrant flycatcher genus *Myiarchus*, only two islands support three sympatric species—the large, ecologically diverse Jamaica and the small uniform Isla Cozumel, off the Yucatán Peninsula of México. Subspecific separation of the Cozumel and mainland populations has been proposed hitherto only in *M. yucatanensis*, but is described here in *M. tyrannulus* and *M. tuberculifer* as well. New subspecies include a second mainland form of *M. yucatanensis*, the Cozumel form of *tyrannulus*, and the Yucatán mainland form of *M. tuberculifer* (the name currently used for this population was based on a holotype from Cozumel). *M. yucatanensis* is non-migratory. Mexican populations of *M. tyrannulus* are migratory; winter records from the Yucatán mainland may be based in large part on migrants from the north. The species is absent from Isla Cozumel in winter, and the winter range of the Cozumel subspecies is unknown. The Yucatán mainland population of *M. tuberculifer* is non-migratory, but the Cozumel subspecies is absent in winter. Its winter range is unknown, but a migrant has been taken near the coast of eastern Honduras. The character states by which the Isla Cozumel subspecies of all three species of *Myiarchus* are defined are virtually identical, although varying in degree of development. There is no clear trend in characters differentiating other Isla Cozumel endemic subspecies; the factors affecting the parallel evolution of the character states of Cozumel *Myiarchus* are unknown.

### INTRODUCTION

Three species of the tyrant flycatcher genus *Myiarchus* (Brown-crested Flycatcher, *M. tyrannulus*; Yucatán Flycatcher, *M. yucata-*

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*nensis*; Dusky-capped or Olivaceous Flycatcher, *M. tuberculifer*, in decreasing order of size) occur sympatrically on Isla Cozumel, off the east coast of the Yucatán Peninsula of México. The only other island within the range of the genus *Myiarchus* that supports three species is the much larger Jamaica (Lanyon, 1967), where there is altitudinal and ecological separation, at least to some extent, among the species (none of which is conspecific with any of the Cozumel forms). Bond (*in litt.*) believes that, in general, "netting of the 3 species of Jamaica *Myiarchus* in the same place would be very unlikely but not impossible," and, indeed, Lanyon (1967) found all three at Good Hope, where he conducted playback experiments. Isla Cozumel is ecologically relatively uniform (other than disturbed versus undisturbed habitats), and all three of its *Myiarchus* species have been captured in the same mist net lane.

In connection with a field study of the comparative ecology of the three Isla Cozumel species (R. B. Waide, in preparation), large series of specimens were borrowed for measuring. It is likely that no comparable series of *Myiarchus* sp. from the Yucatán area had ever been assembled previously; in addition, the material included a significant number of recently collected specimens in freshly molted plumage, as contrasted to the older, mostly worn spring and summer specimens in most museum series. I therefore examined the specimens assembled for Dr. Waide's interspecific study to see if there is intraspecific variation in the Yucatán area, overlooked by earlier workers because of inadequate material.

The Isla Cozumel population of *Myiarchus yucatanensis* has already been described as *M. y. lanyoni* by Parkes and Phillips (1967). The present study revealed that there is also geographic variation in this species on the mainland of the Yucatán Peninsula, among populations all previously considered *M. y. yucatanensis*. In addition, the Isla Cozumel populations of both *M. tyrannulus* and *M. tuberculifer* are subspecifically separable from those of the mainland, although not as dramatically so as in *M. yucatanensis*. The color differences between island and mainland populations of all three species show remarkable similarities; in other words, the differentiation of the three species has taken parallel routes.

#### *MYIARCHUS YUCATANENSIS*

This species is endemic to the Yucatán area, and seems to be a relict form of uncertain relationships within the genus *Myiarchus* (Lanyon, 1965). Neither Lanyon (1965) nor Parkes and Phillips (1967) noted any geographic variation in color within the range attributed to *M. y. yucatanensis* (that is, the peninsular mainland), but when the series

assembled for Dr. Waide's study was arranged geographically, such variation immediately became apparent.

Geographic variation in several species of birds within the Peninsula tends to be correlated with climatic/vegetational zones. Several attempts at classifying such zones were summarized by Paynter (1955:10–15). Details vary, but there is general agreement that rainfall is greatest in the eastern and southern portions (García, 1965) and that vegetation reflects this pattern. Paler subspecies of birds tend to inhabit the more xeric areas to the north, and darker subspecies the more humid areas to the south and east (Paynter, 1955; Parkes, 1974). This pattern is also true of *Myiarchus yucatanensis* on the mainland, and the population of Isla Cozumel, which, with an annual rainfall of 1570 mm, is probably the most humid locality in the peninsular area (Waide, personal communication), is the darkest of all Yucatán Flycatchers and among the darkest of all *Myiarchus*.

The type locality of *Myiarchus yucatanensis* Lawrence is Mérida, in the northern state of Yucatán. The darker form from the humid area of the peninsula thus requires a name. It may be called:

*Myiarchus yucatanensis navai*, new subspecies

*Holotype*.—CM 142205, adult female from 8 km NNE of Chetumal, Quintana Roo, México, collected by Santos Farfán B. and prepared by Juan Nava S. for Kenneth C. Parkes, on 1 February 1965 (field no. KCP 2332).

*Characters*.—To some extent intermediate in color between *M. y. yucatanensis* and *M. y. lanyoni*. The throat and breast of *navai* are slightly darker gray than in *yucatanensis* but not as dark as in *lanyoni*, and the lower breast lacks the olivaceous tinge of *lanyoni*, being, if anything, slightly washed with brownish. The gray of the anterior underparts extends farther posteriorly than in *yucatanensis* and the gray of the sides and flanks restricts the extent of the yellow of the abdomen, as in *lanyoni* but somewhat less extensively (in well made skins of *yucatanensis*—not understuffed so that the sides are pulled together toward the middle—the gray of the sides hardly shows beyond the folded wings, whereas in *navai* and even more in *lanyoni*, the gray of the sides extends medially). The sides and flanks are a clearer, less greenish gray than those of *lanyoni*. The abdomen color, season for season (this area fades rapidly—see Parkes and Phillips, 1967, for details), is paler than in *yucatanensis* and not noticeably different from that of *lanyoni*.

Dorsally *navai* is darker than *yucatanensis*, but freshly molted birds lack the blackish cast of *lanyoni*. The back of *navai* is browner, less greenish than in *yucatanensis*, and thus contrasts less with the brown

of the crown, which is distinctly darker, more chocolate and less reddish brown than in the nominate race.

The effect of dorsal fading with season is shown by the fact that two 20 April skins of *lanyoni* are scarcely darker above than September and October specimens of *navai*. The April *navai* are immediately identifiable as such, however, by the relative extent of the yellow abdominal area. Similarly, the distinction between *navai* and *yucatanensis* in dorsal coloration is much less obvious in worn and faded specimens.

*Range*.—Southern Quintana Roo and southeastern Campeche, México, northern Petén (Guatemala), and probably northern Belize (Russell, 1964). For a discussion of intergradation with nominate *yucatanensis*, see *Remarks*, below.

*Etymology*.—It is a pleasure to dedicate this new subspecies to Sr. Juan Nava Solorio, now of Bacalar, Quintana Roo, México, who accompanied me during most of my Mexican field work, and whose indefatigable persistence on Isla Cozumel provided the holotype of *Myiarchus yucatanensis lanyoni*.

*Remarks*.—Only two specimens from southeastern Campeche have been examined—28 km N (CM) and 8 km W (UW) of Xpujil. Unfortunately, the first of these is a "dilute" freak as far as its brown pigments are concerned. The other is a badly shot specimen in very heavy first prebasic molt. However, the extreme amount of gray and the reduction of yellow on the underparts of the CM specimen, and the darkness of the new dorsal feathers of the UW specimen, indicate that the SE Campeche population is, not surprisingly, assignable to the race of adjacent southern Quintana Roo.

Specimens from western and southwestern Campeche are nearest *navai* but variably intermediate toward *yucatanensis* in dorsal color. Ventrally, the throats of these birds are as pale gray as in *yucatanensis*, but abdomen color in seasonally comparable specimens is nearer *navai*. The extent of gray on the sides and flanks is intermediate between the two races.

Three specimens (USNM) from coastal northeastern Quintana Roo (Puerto Morelos, 2; La Vega, 1) are unfortunately old (1901) and seasonally rather faded (March). However, the color of the underparts clearly matches *navai*. The two Puerto Morelos specimens are not separable from March *yucatanensis* dorsally, but the La Vega specimen is fully as dark as comparable material of *navai*. Two specimens from Tabi (Taabi), central Quintana Roo (YPM, MCZ) resemble the Puerto Morelos specimens in matching *navai* ventrally and *yucatanensis* dorsally.

The Yucatán Flycatcher is known from northern Belize only from sight (and sound) records (Russell, 1964). Occurrence in this area



would be expected, and this population is undoubtedly referable to *navai*.

*Specimens examined.*—*M. y. yucatanensis*: MÉXICO: Yucatán: Chemax, 1; Chichén Itzá, 21; Progreso (14½ km S), 2; Temax, 1; Tunkas, 1; Xocempich, 3; unspecified, 7. *M. y. yucatanensis* × *navai*: MÉXICO: Quintana Roo: Puerto Morelos, 2; Tabi, 2. Campeche: Champotón and vicinity, 6; Ichek, 1; Matamoros, 1; Pacaitun, 2. *M. y. navai*: MÉXICO: Quintana Roo: Chetumal and vicinity, 3; La Vega, 1. Campeche: Xpujil (8 km W), 1; Xpujil (28 km N), 1. GUATEMALA: Petén: Tikal, 1. *M. y. lanyoni*: MÉXICO: Quintana Roo: Isla Cozumel (various localities), 11.

#### MYIARCHUS TYRANNULUS

Of this, the largest of the *Myiarchus* flycatchers of the Yucatán area, all of the Mexican populations of the Caribbean slope from the lower Rio Grande through the Yucatán Peninsula (including Isla Cozumel), and those of Belize, eastern Guatemala, and mainland Honduras, have been assigned to *M. t. cooperi* Baird, the holotype of which is a Verreaux specimen from "Mexico" (Deignan, 1949). Paynter (1955:194) stated that this species is found "throughout the [Yucatán] Peninsula, including Isla Cozumel, during all seasons." As the northern populations of this subspecies are known to be migratory, it is difficult to be certain of the status of the winter records from the mainland of the Yucatán Peninsula. Paynter's inclusion of Isla Cozumel in his statement of presence "during all seasons" is puzzling. I have seen no winter specimens, and we failed to find the species on Cozumel during a thorough search in two and a half weeks of November 1965, nor had we found it during an earlier visit 20–23 January 1965. Bond (1961) observed *Myiarchus tyrannulus* on Isla Cozumel in mid-February 1961, and Waide (personal communication) did not see it before 1 March in 1979. The return of the first migrants to the island is thus presumably between late January and early March, unless Bond's birds were wintering stragglers from the north. According to unpublished observations made in 1977, 1978, and 1979 by Barbara MacKinnon de Montes, this species was seen on Isla Cancún (ca. 50 km N of Isla Cozumel) only between 2 April and 21 August. In Gallon Jug, northwestern Belize, E. O. Willis was in residence from 15 February to 1 August 1957, but saw *Myiarchus tyrannulus* only from March through July, and S. M. Russell saw obvious northbound migrants on Calabash Cay, off Belize, on 9 and 10 April 1956 (Russell, 1964). It thus appears certain that the insular populations of this species in the Yucatán area are migratory. In addition, many of the midwinter records of this species on the Yucatán Peninsula may pertain to individuals originating farther north. Unfortunately this cannot be documented through geographic variation, as I have been unable to distinguish among specimens from the various parts of the generally

accepted range of *M. t. cooperi*, with the sole exception of those from Isla Cozumel. If some or all of the Yucatán Peninsula population of *Myiarchus tyrannulus* does, indeed, depart in the late summer or fall (as appears to be true of the populations of Islas Cozumel and Cancún and of northern Belize), it is replaced by wintering birds taxonomically indistinguishable from the breeding population.

Lanyon (1960) stated that *Myiarchus tyrannulus* had not differentiated on Isla Cozumel, but did not indicate the extent of his comparative series. He recognized *M. t. insularum* Bond of the Honduras Bay Islands, which is *less* strongly differentiated from *cooperi* than is the undescribed Isla Cozumel population, which may be called:

*Myiarchus tyrannulus cozumelae*, new subspecies

*Holotype*.—CM 143356, adult male from Cedral, Isla Cozumel, Quintana Roo, México, collected by Juan Nava S. for Kenneth C. Parkes, on 19 April 1968 (field no. KCP 3064).

*Characters*.—Similar to *M. t. cooperi* of the adjacent mainland (and elsewhere) in size, but distinctly darker and browner, less greenish above, with (especially) crown and upper tail coverts darker, richer brown; rufous inner margins of rectrices darker; gray of upper breast tending to invade yellow of lower breast; posterior underparts in general slightly paler yellow; axillars distinctly more whitish, less yellow (in *extremely* worn and faded specimens, the axillar color and the extent of gray on the chest may be the only reliable characters). Nearer *M. t. insularum* of the Bay Islands of Honduras in dorsal color, but even darker than that race; otherwise differs from *insularum* as from *cooperi*. Bond (1936) described *insularum* as having underparts averaging slightly darker than in *cooperi*, but he had only three specimens of the former (and an unspecified number of the latter). The much larger CM series shows that *insularum* does not differ from *cooperi* in either the gray of the throat and breast or the yellow of the abdomen. The subspecies *insularum* is, in fact, intermediate between *cooperi* and *cozumelae* in color, matching the former in ventral color and approaching the latter in dorsal color.

*Range*.—Known to breed only on Isla Cozumel, Quintana Roo, off the east coast of the Yucatán Peninsula, México; Isla Cancún specimens should be examined. Winter range unknown.

*Etymology*.—Named for the island it inhabits.

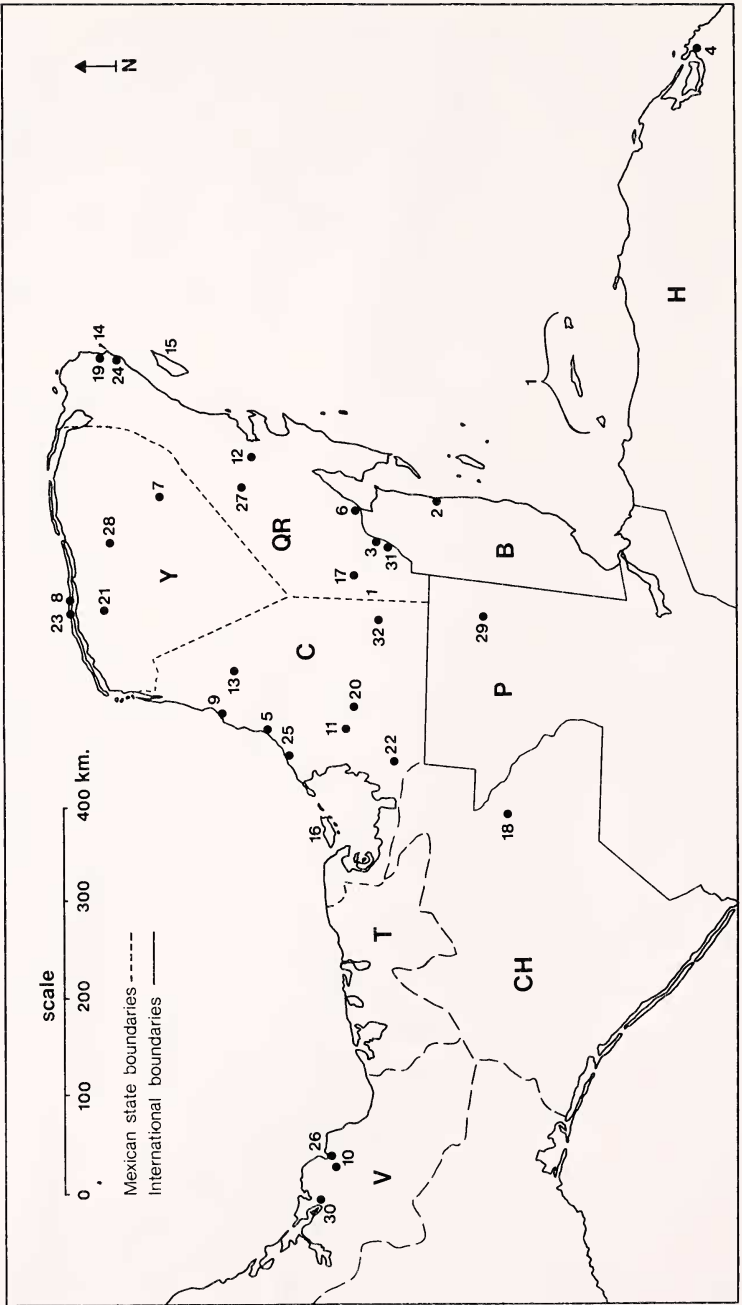
*Remarks*.—Although the color differentiation of the Isla Cozumel population of *Myiarchus tyrannulus* is much less striking than that of *M. yucatanensis*, some interesting parallel tendencies may be noted. Although *M. t. cozumelae* does not approach the dorsal blackness of *M. y. lanyoni*, nevertheless it is both darker and browner than its

mainland relative. Both *cozumelae* and *lanyonii* share the invasion of gray into the yellow of the posterior underparts, although in *cozumelae* this invasion does not extend as far posteriorly along the sides as in *lanyonii*. Both of the Cozumel races have whitish rather than yellow axillars. Finally, although differences in the yellow of the underparts were not mentioned in the original description of *M. y. lanyonii* (Parkes and Phillips, 1967), the addition of the fresh-plumaged series taken by Waide shows that in *lanyonii* the yellow is noticeably paler than that of the mainland nominate race, just as is true of *M. t. cozumelae* versus *M. t. cooperi*. There is no character in which *M. t. cozumelae* differs from *M. t. cooperi* that is not similarly or more strongly differentiated in *M. y. lanyonii* as compared with *M. y. yucatanensis*.

*Specimens examined*.—*M. t. cooperi*: TEXAS: Brownsville, 2; Cameron Co. unspecified, 2. MÉXICO: Tamaulipas: Alta Mira, 3. Veracruz: Catemaco and vicinity, 3. Chiapas: Mapastepec (10 km N), 1. Yucatán: Chichén Itzá, 6; Chicxulub Puerto, 1; Dzidzantún, 1; Mérida, 1; Progreso (9–14 km S), 3; San Felipe, 1; Santa Clara, 1; Temax, 1; Xbec, 1; unspecified, 2. Quintana Roo: Chetumal, 6; La Vega, 1; Tabi, 1. Campeche: Champotón, 2; Isla del Carmen, 4. BELIZE: various localities, 10. HONDURAS: various mainland localities, 19. *M. t. insularum*: HONDURAS: Bay Islands (various), 22. *M. t. cozumelae*: MÉXICO: Quintana Roo: Isla Cozumel (various localities), 11.

#### *MYIARCHUS TUBERCULIFER*

This is the smallest and most abundant of the *Myiarchus* flycatchers in the Yucatán Peninsula and adjacent areas. The species as a whole, like *M. tyrannulus*, is found from the southwestern United States to Argentina and Brazil, but it has been much more plastic than *tyrannulus*. Traylor (1979) admitted twelve subspecies of *tuberculifer* and only six of *tyrannulus*. Within the area occupied by the two northern subspecies *M. tyrannulus magister* (Pacific) and *M. tyrannulus cooperi* (Caribbean), five subspecies of *M. tuberculifer* were admitted by Traylor. This contrast in plasticity may well be associated with increased opportunity for gene flow in the strongly migratory *tyrannulus*; only the northwesternmost subspecies of *tuberculifer*, *M. t. olivascens*, has been considered migratory. In such a plastic species as *Myiarchus tuberculifer*, it is hardly surprising to find that the Isla Cozumel population, contrary to current usage, is subspecifically separable from that of the adjacent Yucatán Peninsula mainland. What is surprising is that the Isla Cozumel population is migratory, whereas that of the mainland is not. In January 1965 we failed to find *M. tuberculifer* on Cozumel, although it was singing abundantly on the mainland, separated only by a 20 km channel. Two and a half weeks of searching for *Myiarchus* on the island in November of the same year yielded only *M. yucatanensis lanyonii*. As we could not believe that the species had become extinct on the island (it had been collected as recently as 8





August 1962; KU 40675), the only viable alternative theory was that, for some unknown reason, *Myiarchus tuberculifer* is migratory on Isla Cozumel. Such proved to be the case; the species was abundant on the island on 19–20 April 1968, in areas from which it had been absent during our January and November visits. The factors underlying this difference between the Cozumel and mainland populations will be discussed by Waide (in preparation).

The name *platyrhynchus* Ridgway is currently used for the Dusky-capped Flycatchers of all of the Yucatán Peninsula and Isla Cozumel. The type locality of *platyrhynchus* is Isla Cozumel, so the mainland subspecies remains to be named. It may be called:

*Myiarchus tuberculifer manens*, new subspecies

*Holotype*.—CM 144800, male just completing first prebasic molt, from ca. 20 km E of Chicxulub Puerto, Yucatán, México, collected by Juan Nava S. for Kenneth C. Parkes, on 2 December 1971 (field no. KCP 3232).

*Characters*.—Similar to *M. t. platyrhynchus* of Isla Cozumel, but dorsum paler, more greenish-olive (less sooty brown), contrasting more with the dark crown; reddish brown of upper tail coverts, outer webs of unworn rectrices, wing coverts, and secondaries paler. Yellow of posterior underparts much richer and more extensive—in *platyrhynchus* the gray of the upper breast extends farther caudad centrally and also blends gradually with the yellow of the lower breast; in addition, the sides and flanks of *platyrhynchus* are washed with grayish olive, narrowing the pure yellow area. In older and seasonally faded specimens of *manens*, the yellow may fade to the pale color typical of *platyrhynchus*, but such specimens are immediately recognizable by the greater extent of yellow on the underparts. The axillars and under wing coverts of *manens* are yellow, those of *platyrhynchus* white or nearly so. In *manens* there is a tendency for the throat to appear light gray streaked vaguely with white; the throat of *platyrhynchus* is paler gray and more uniform. The lower mandible of *manens* is brownish in

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Fig. 1.—Principal localities mentioned in text. B = Belize; C = Campeche, México; CH = Chiapas, México; H = Honduras; P = Petén, Guatemala; Q = Quintana Roo, México; T = Tabasco, México; V = Veracruz, México; Y = Yucatán, México; 1 = Bay Islands; 2 = Belize City; 3 = Camp Mengel; 4 = Cauquira; 5 = Champotón; 6 = Chetumal; 7 = Chichén Itzá; 8 = Chicxulub Puerto; 9 = Ciudad Campeche; 10 = Coyame; 11 = Escárcega; 12 = Felipe Carrillo Puerto; 13 = Ichek; 14 = Isla Cancún; 15 = Isla Cozumel; 16 = Isla del Carmen; 17 = Laguna Chacabacab; 18 = Laguna Ocotol; 19 = La Vega; 20 = Matamoros; 21 = Mérida; 22 = Pacaitún; 23 = Progreso; 24 = Puerto Morelos; 25 = Sabancuy; 26 = Sontecomapan; 27 = Tabi; 28 = Temax; 29 = Tikal; 30 = Tlacotalpan; 31 = Xcopan; 32 = Xpujil.

life, thus differing from that of *platyrhynchus* and of *connectens* and *lawrenceii*, the adjacent mainland races, which are black.

*Range*.—All but the base of the Yucatán Peninsula, México. See *Remarks*, below, for a discussion of intergradation.

*Etymology*.—From the Latin verb *maneo*, to remain or stay in place, in reference to its non-migratory status as contrasted with *M. t. platyrhynchus*.

*Remarks*.—As mentioned in the introductory remarks on this species, true *platyrhynchus* of Isla Cozumel leaves its breeding ground for the winter, as is also true of *M. tyrannulus cozumelae*. The wintering area of neither subspecies is known, but there is one indication of the migration route of *platyrhynchus*. Monroe (1968:283) reported a specimen of *Myiarchus tuberculifer* he collected on 13 April 1964 in a mangrove swamp near Cauquira, on Laguna Caratasca, just inland from the northeasternmost coast of Honduras. This specimen, a male "in breeding condition," he was unable to separate from "examples of *M. t. platyrhynchus* Ridgway from the Yucatán Peninsula and [it] extends the known range of this race south of British Honduras." As indicated by Monroe's map, such a "range extension" would result in a totally disjunct pattern, as the remainder of Caribbean Honduras is occupied by the subspecies *connectens* Miller and Griscom. Monroe, of course, was aware neither that "*platyrhynchus*" as then understood was a composite nor that true *platyrhynchus* of Isla Cozumel is migratory. I have examined his specimen (LSU 32348) and find that it matches Cozumel specimens in every respect. The fact that his specimen was in "breeding condition" can be explained by the late date; Nelson and Goldman (specimens in USNM) found Dusky-capped Flycatchers already on Isla Cozumel 4–8 April 1901. Monroe's bird would have had about 670 km farther to fly if it had gone on a direct diagonal from the collecting locality across the Caribbean to Isla Cozumel, or about 1150 km if it followed the coastline west to the end of the Gulf of Honduras and then turned north along the Belize and Quintana Roo coasts. We still lack information as to the true winter range of *platyrhynchus*.

The range of *manens* adjoins that of *connectens* at the base of the Yucatán Peninsula. The latter race differs from both *manens* and *platyrhynchus* in having the outer edge of the inner webs of the rectrices distinctly rufous, as well as in having a darker back and a decidedly darker and more contrasting crown. It also has the throat darker, less whitish gray than in *manens*. The first signs of intergradation appear in the interior of Quintana Roo. Three poorly-made skins (March, May, June; 2 Tabi, 1 Felipe Carrillo Puerto) from this area are faintly darker on the crown than similarly worn specimens from Chichén Itzá, in the interior of the state of Yucatán to the north, but otherwise they

show no approach to *connectens*. Of eight skins from southeastern Quintana Roo (vicinity of Chetumal; Xcopan; Camp Mengel; Laguna Chacanbacab), four show very narrow reddish-brown edgings on the inner webs of the rectrices. All are darker and somewhat browner dorsally than more northern birds, all have darker throats, and most have the crowns darker and contrasting more with the back. These character states are not necessarily coordinated. The specimen with the least *connectens*-like crown is YPM 8722, from 46 km W of Chetumal, 15 February 1949. It is also relatively pale and less brownish dorsally than most of this series, but is one of the four with narrow rufous inner margins to the rectrices. YPM 8721, from Laguna Chacanbacab, 14 May 1949, in spite of the late spring date when fading would be expected, is the darkest and brownest dorsally of the series, but it lacks the rectrix edgings. The whole series can be considered to be intergrades between *manens* and *connectens*, which is compatible with Russell's (1964) identification of most of the Dusky-capped Flycatchers from Belize south to about Belize City as intergrades (although one specimen from Corozal, near Chetumal, he called "*platyrhynchus*" [= *manens*]).

The northernmost specimen examined from the state of Campeche is one from Ichek (YPM 13796), which is typical of *manens*. Two from San José Carpizo, 45 km S of Ciudad Campeche (UMMZ 155762-3) also belong here. Farther south, one of three specimens from 8-32 km W of Escárcega and one from La Tuxpeña have traces of rufous on the inner webs of the rectrices and are slightly darker on the crown than typical *manens*, but are closest to that race. Their intergradation is with *connectens* rather than with the similarly colored but much larger race *lawrenceii* (Giraud) of the Caribbean slope of México to the west, as the intergrades are identical in size with both *manens* and *connectens*. Following the coast south and west from Ciudad Campeche, a specimen from Champotón is nearest *manens* dorsally, but has narrow distinct rufous inner edges to the rectrices and a slightly darker throat. One from Sabancuy, however, does not differ from *manens*. An excellent series of 13 January and February specimens from Isla del Carmen is quite variable in all color characters but not in size, and must therefore be considered *manens*  $\cong$  *connectens*. Finally, a specimen from La Curva, 34 km E of the Tabasco border, is similarly intermediate.

Three specimens from Tikal, Petén, Guatemala, about 60 km S of the Campeche border (MCZ) are *connectens*. Smithe and Paynter (1963) called these "*platyrhynchus*" [= *manens*], stating that all lacked "rufous markings on the underside of the rectrices." All are very dark and brownish dorsally and have blackish caps. One September specimen (MCZ 262919) has (contra Smithe and Paynter, 1963) obvious

rufous edges to the inner webs of the rectrices, whereas in a June specimen (260992) these have been almost completely worn away. Another June skin (260993), with a surprisingly unworn tail, lacks the rufous on the tail, and in this respect resembles some of the Belize skins that are otherwise typical of *connectens*. A single skin from the ruins of Chicama, 8 km W of Xpujil, southeastern Campeche, 8 August 1978 (UW A20278), in heavy molt, is indistinguishable from *connectens*.

Paynter (1957) showed that the Dusky-capped Flycatchers of Laguna Ocotol, in easternmost Chiapas near southwestern Petén, are *connectens*; Traylor (1979) mentioned Chiapas only in the range of *lawrenceii*.

Paynter (1957) referred several times to *connectens* as larger than "*platyrhynchus*" [= *manens*], and measurements published by Brod-korb (1943) show only 1 mm overlap in wing measurements of these two races. The specimens assembled for this study, however, show only a slight difference in mean in both wing length and weight between the two races, with the extremes almost identical. The overemphasis on size as a character separating *manens* and *connectens* is exemplified by Smithe and Paynter (1963), who, as mentioned above, identified their five Tikal specimens as "*platyrhynchus*." I have seen three of these, and all three matched *connectens* perfectly in all color characters with the exception of one specimen that lacked rufous on the inner margins of the rectrices. Smithe and Paynter stated that their series "is quite dark, thereby approaching *M. t. connectens*, but all the specimens are small . . ." (emphasis added). Rather than the small size being an indication of the necessity of identifying these dark birds as "*platyrhynchus*," it is simply further evidence that the size difference between the Yucatán subspecies and *connectens* is insignificant. Paynter's specimens from Laguna Ocotol, Chiapas, which averaged slightly larger than Yucatán Peninsula specimens in both weight and wing length, may have been affected by introgression from *lawrenceii*. The two subspecies *lawrenceii* and *connectens* differ only in size, with northern examples of the former being decidedly larger than *connectens*. Traylor (1979) mentioned only El Salvador as an area of intergradation between the two, and gave the range of *lawrenceii* as extending to "Tobasco and Chiapas, and highlands of Guatemala." The intergradation in size between *lawrenceii* and *connectens* is more clinal than this range description would suggest, and begins farther north than indicated by Traylor, as already shown by Wetmore (1943) and Brod-korb (1943), extending to southern Veracruz. This is confirmed by specimens examined in this study; those from Tlacotalpan and Son-tecomapan, southern Veracruz, were smaller than *lawrenceii* from northeastern México but larger than Honduras specimens of *connectens*.



Paynter (1957) was correct in stating that "*platyrhynchus*" tends to have a paler "bill" [=lower mandible] than *connectens* or *lawrenceii*, but only if this statement is restricted to the *manens* or mainland component of Paynter's composite "*platyrhynchus*." In true *platyrhynchus* of Isla Cozumel, the USNM series taken by Nelson and Goldman in 1901 has pale brown lower mandibles, but in specimens taken between 1962 and 1979, the lower mandibles are black. In *manens* of the peninsular mainland, however, pale lower mandibles are not correlated with museum age, as indicated by color notes taken at the time of collecting by Paynter and by A. R. Phillips; in these, the lower mandibles are quite consistently brownish. I agree with Russell (1964) that this character is not wholly diagnostic. There is so much variation in the color of *dried* (specimen) bills that the character is of little use in evaluating intergradation when original color notes are lacking (as is usually the case). The separation of *M. t. platyrhynchus*, *manens*, and *connectens* by plumage color is sufficiently clearcut for bill color to be unnecessary for definition of these races.

*Specimens examined*.—*M. t. lawrenceii* (+ *lawrenceii* × *connectens*): MÉXICO: Tamaulipas: Río Corona, 1; Victoria, 1. Nuevo León: Mesa de Chipinque, 1. Hidalgo: Jacala, 1. Veracruz: Coyamé, 5; Sontecomapan (1 mi NW), 2; Tlacotalpan (7–8 mi E), 2. *M. t. connectens*: MÉXICO: Campeche: Ruins of Chicama, 1. GUATEMALA: Petén: Tikal, 3. BELIZE: various localities, all S of Belize City, 19. HONDURAS: various localities, 38. *M. t. connectens* × *manens*: MÉXICO: Campeche: Champotón, 1; Isla del Carmen, 14; La Curva, 1. Quintana Roo: Camp Mengel, 1; Chetumal and vicinity, 5; Laguna Chacanbacab, 1; Xcopan, 1. *M. t. manens*: MÉXICO: Campeche: Escárcega (8–32 km W), 3; Ichek, 1; La Tuxpeña, 1; Sabancuy, 1; San José Carpizo, 2. Yucatán: Chichén Itzá, 23; Chicxulub Puerto and vicinity, 4; Progreso (1–16 mi E), 5; Sisal, 3; Uxmal, 2. Quintana Roo: Felipe Carrillo Puerto, 1; Kantunil-kin (15 km NW), 1; La Vega, 1; Xcan, 2. *M. t. platyrhynchus*: MÉXICO: Quintana Roo: Isla Cozumel (various localities), 14. HONDURAS: Gracias a Dios: Cauquira (1 mi SE), 1.

## DISCUSSION

Of the three *Myiarchus* flycatchers sympatric on the island of Jamaica, one (*M. validus*) is a well differentiated species that has even been generically separated in the past; one (*M. barbirostris*) is closely related to the widespread *M. tuberculifer* but considered a separate species because of differences in vocalizations; and one (*M. stolidus*) is a member of a West Indian superspecies of unknown mainland affinities (Lanyon, 1967). In contrast, all three of the sympatric *Myiarchus* on Isla Cozumel are only subspecifically differentiated from their representatives on the adjacent mainland of the Yucatán Peninsula. Two (*M. tyrannulus cozumelae* and *M. tuberculifer platyrhynchus*) are migratory on Isla Cozumel, although the mainland representative of the latter (*M. tuberculifer manens*) is not. The third Cozumel form, *M. yucatanensis lanyoni*, is an exceptionally distinctly differentiated insular representative of a relict species of uncertain affinities within

the genus; like its mainland relatives, *M. y. lanyoni* is non-migratory. The Isla Cozumel subspecies of *Myiarchus yucatanensis* was described as differing from the nominate population of the mainland in being very much darker (blackier) dorsally; in having the rufous markings of wings and tail darker; in having the gray of the lower breast less pure and more extensive posteriorly, extending along the sides and flanks such that the yellow area of the abdomen is restricted; and in having the under wing coverts and axillars "dull yellowish white rather than light yellow." As stated earlier in the present paper, examination of additional specimens has shown that the yellow of the underparts is distinctly paler than in specimens of the nominate race of comparable season and museum age. Although differing in degree of differentiation, each of these character states is matched in the Isla Cozumel populations of *M. tyrannulus* and *M. tuberculifer*. In both, the Cozumel subspecies is darker and browner, less greenish dorsally; the rufous areas of upper tail coverts, wings and tail are darker (except for the wings of *M. tyrannulus cozumelae*, in which the rufous is not darker, and the tail of *M. tuberculifer platyrhynchus*, which, like mainland *manens*, lacks significant rufous areas); the gray of the lower breast is more extensive and blends more with the adjacent yellow; the yellow is paler; and the axillars (and under wing coverts in *M. tuberculifer platyrhynchus*) are white or whiter, less yellowish.

Parallel geographic variation in color in congeneric species has been described for several birds. Of the Downy Woodpecker (*Picoides pubescens*) of North America, Baird et al. (1874) wrote: "The remarks already made on the variation of [the Hairy Woodpecker, *P. villosus*] apply equally well here; all the differences in size and markings with locality being almost exactly reproduced." Snow (1954) called attention to parallel patterns of color variation in *Parus cristatus*, *P. palustris*, and *P. montanus* in Europe. Such variation is often associated with fairly obvious environmental conditions—for example, the desert-colored larks of North Africa (cf. *Galerida cristata* and *G. theklae*; Etchécopar and Hüe, 1964) and the heavily pigmented races of the above-mentioned Downy and Hairy woodpeckers in the humid Pacific Northwest of North America. However, there is no obvious major difference between the environmental conditions on Isla Cozumel and the adjacent Yucatán Peninsula mainland that could be correlated with the color trends visible in *Myiarchus*. Paynter (1955) recognized Isla Cozumel endemic subspecies of the following Yucatán Peninsula species (excluding those of West Indian affinities or of questionable Cozumel provenience): *Buteo magnirostris*, *Crax rubra*, *Chlorostilbon canivetii*, *Melanerpes aurifrons*, *M. pygmaeus*, *Attila spadiceus*, *Melanoptila*

*glabrirostris*, *Polioptila caerulea*, *Cyclarhis gujanensis*, *Piranga ro-seogularis*, *Cardinalis cardinalis*, and *Tiaris olivacea*. Of these, the *Crax* and *Melanoptila* differ from the mainland populations only in size, and the *Chlorostilbon* in tail proportions. In *Piranga* and *Cardinalis* there is geographic variation on the mainland; the Cozumel population of *Piranga* is nearer the darker mainland race, whereas that of *Cardinalis* is nearer the paler mainland race. The *Tiaris* differs from the mainland race in having less extensive black on the underparts of males. Only in *Buteo*, both *Melanerpes*, *Attila*, *Polioptila*, and *Cyclarhis* can the Cozumel populations be broadly characterized as darker dorsally than those of the mainland, and these differ sufficiently *inter se* as to the manifestation of richer pigmentation that it is doubtful that they represent any trend that is common to the three *Myiarchus* species. One looks in vain for any counterpart to the pale yellow underparts of the three Cozumel *Myiarchus* races.

It is clear that within the rather uniform genus *Myiarchus*, selection has operated on three species (not especially closely related *within* the genus) on Isla Cozumel in virtually identical fashion. Other Cozumel endemic subspecies show little or no evidence of similar responses to selection. The environmental factors to which the parallel trends in differentiation in *Myiarchus* have responded remain obscure.

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